

There's more behind it: Perceived depth order biases perceived numerosity/density

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Humans have a clear sense of the numerosity of elements in a surface. However, recent studies showed that the binding of features to the single elements is severely limited. By studying the relationship of depth order and perceived numerosity of overlapping, pseudotransparent surfaces, we show that the binding of elements to the surfaces is also limited. In transparent motion, anisotropies for perceived depth order and perceived numerosity were highly correlated: directions that were more likely to be perceived in the back were also more likely to be perceived as more numerous. The magnitude of anisotropies, however, was larger for depth order than for numerosity, and the correlation with eye movement anisotropies also developed earlier for depth order than for numerosity judgments. Presenting the surfaces at different disparities removed the anisotropies but lead to a consistent bias to overestimate the numerosity of the surface in the back and to underestimate the surface in the front. The magnitude of this bias did not depend on dot density or lifetime. However when the speed of motion was reduced or when the two surfaces were presented at different luminance polarities, the magnitude of anisotropies and the numerosity bias were greatly reduced. These results show that the numerosity of pseudotransparent surfaces is not processed independent of the depth structure in the scene. Instead there is a strong prior for higher numerosity in the back surface.

Keywords: numerosity, density, depth order, transparent motion, anisotropies, smooth pursuit eye movements, binocular disparity

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Introduction

When a cloud of moving dots contains two distinct motion directions, observers typically group the dots according to their motion direction and perceive two transparent surfaces, moving across each other. Although the moving dots in transparent motion displays are perceptually grouped by motion direction, it is not clear whether this grouping is perfect. One way to test the accuracy of the perceptual grouping is to measure the perceived relative numerosity of the two overlapping surfaces. If the grouping of dots is accurate, observers should be able to perceive the relative numerosity of overlapping surfaces veridically.

Theoretically, the numerosity of each surface could be determined locally, by assigning each dot to a surface and by summing up the dot count for each surface separately. Alternatively, the numerosity of a surface might be an inherent property of the surface itself, which is accessible without reference to the single dots. The perception of transparency in a display with two motion directions seems to be based on a local computation, since it can be eliminated completely if dots of the two motion directions are paired locally (Qian & Andersen, 1994). Furthermore, transparency is analyzed early, before color and motion direction are

paired, because transparency facilitates the perceptual binding of these stimulus features (Clifford, Spehar, & Pearson, 2004; Moradi & Shimojo, 2004). These findings suggest that the segmentation of surfaces precedes the extraction of other features. In that view numerosity might also be computed after the surface segmentation, as a global property of the surfaces.

There is some evidence that the binding of features to single elements in a larger crowd can be greatly impaired by motion. Continuous color changes in a set of dots become practically invisible when the dots start to move (Suchow & Alvarez, 2011). In motion transparency, abrupt changes of dot color can go unnoticed, as long as the proportion of colors across dots remains the same (Saiki & Holcombe, 2012). Dot color and motion direction can be misbound altogether in the periphery, when a conflicting stimulus is presented in the central retina (Wu, Kanai, & Shimojo, 2004). Furthermore, transparent motion is perceived, even when individual dots alternate between two motion directions (Kanai, Paffen, Gerbino, & Verstraten, 2004). This means that the motion direction of the single dots is not tracked, only the coherent global motion of the whole group of dots. In structure-from-motion displays, which are similar to transparent motion displays, observers only detect very large holes in the surfaces (Treue, Andersen, Ando, & Hildreth,

1994). This finding also points in the direction that the surfaces are interpolated and the identity of single elements is lost. In the light of these results, it is questionable whether the binding of single dots to the surfaces is very reliable. Here we investigated this issue by manipulating the dot number in the two surfaces and by asking observers to judge their relative numerosity.

Although all dots are displayed at the same depth in motion transparency, observers see one surface in the front and another surface in the back. This depth order of the surfaces is inherently ambiguous, and it has been shown that there are strong anisotropies in depth order preferences (Mamassian & Wallace, 2010; Schütz, 2011), so that some motion directions are more likely to be perceived in the back than others. The perceived depth order also can be biased by a range of surface properties, like dot speed, dot size, or dot number (Moreno-Bote, Shpiro, Rinzel, & Rubin, 2008; Schütz, 2011). Since dot number biases the perceived depth order, we furthermore investigated in this study, whether this interaction is bidirectional, i.e., whether perceived depth order also affects perceived numerosity. To this end we asked observers to indicate the perceived depth order of the surfaces and also experimentally manipulated the relative disparity between the two surfaces.

Methods

Observers

The author and 11 naive observers participated in these experiments (four men and eight women, aged between 20 and 31 years). The naive observers were students of the Justus-Liebig-University Giessen and were paid for participation. Experiments were in accordance with the principles of the Declaration of Helsinki and approved by the local ethics committee LEK FB06 at the University Giessen (Proposal Number 2009-0008). Experiment 1 was performed by 12 observers, Experiments 2–4 were performed by 11 observers, Experiment 6 by nine observers and Experiments 5 and 7 by 10 observers.

Experiments

In Experiment 1, we presented transparent motion without disparity and asked observers to indicate the motion direction perceived in the back or the motion direction perceived as more numerous (Figure 1A). The two perceptual tasks were collected in separate conditions to avoid interference between the tasks.

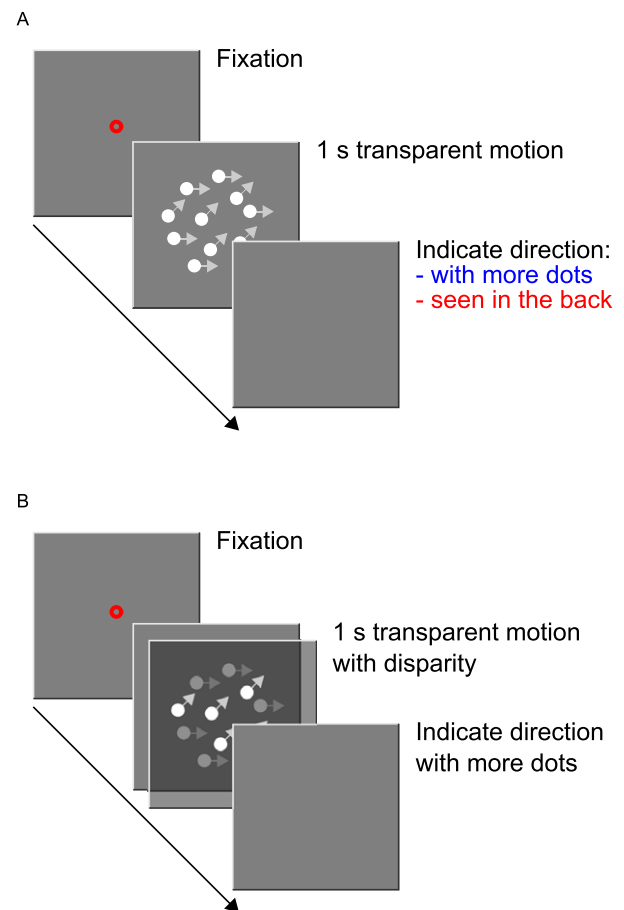


Figure 1. Experimental paradigms. Stimuli are not drawn to scale. (A) Experiment 1. Depth order and numerosity judgments were measured in separate conditions. (B) Experiments 2 to 6. The two surfaces were presented at different disparities. In Experiment 6, the two surfaces had additionally opposite luminance polarity.

Eye movements were recorded to measure the time course of the perceptual decisions. In Experiment 2, we presented the transparent motion either without or with 7.4 arcmin relative disparity between the two surfaces (Figure 1B). In Experiment 3, the relative disparity was 3.7, 11.0, or 25.7 arcmin. In this experiment even the smallest relative disparity of 3.7 arcmin was above the typical stereoacuity thresholds of about 0.5 to 2 arcmin (for review see Arditi, 1986). Cursorsy measurements with five observers showed that all observers were 100% correct at discriminating the two surfaces at a relative disparity of 3.7 arcmin. In Experiment 4, the overall dot density was 0.25, 0.5, 1, or 2 dots/degrees of visual angle (dva^2). In Experiment 5, the speed of the dots was 0, 5, or 10 dva/s and the dot lifetime was unlimited or 200 ms. Experiment 6 was identical to Experiment 2, except that the two surfaces always had opposite luminance polarities. Due to this manipulation, dots could not only be assigned to the two surfaces by motion direction and disparity, but also by luminance polarity and/or by luminance contrast. In

Experiment 7, a comparison surface, which was presented alone, had to be compared to a standard surface, which was either presented in front or behind an inducing surface (Figure 7A). The two possible depth orders of the standard and the inducing surface were presented in separate sessions, so that the observers knew in advance, which depth plane they had to attend to. The position of the standard and comparison surface (left or right) was randomized.

Visual stimuli

A random-dot kinematogram (RDK) appeared within a circular aperture of 10 dva radius, except for Experiment 7, where the radius was 9 dva and two apertures were presented at 10 dva horizontal distance from center to center. Black and white dots ($0.14 \text{ dva} \times 0.14 \text{ dva}$) were presented on a gray background. The luminance polarity of the dots was randomized for each trial. All dots had the same luminance polarity in a given trial, except for Experiment 6, in which the two surfaces always had opposite luminance polarities. The dots moved at 10 dva/s and had a limited life time of 200 ms, except for Experiment 5, in which the speed and the lifetime of the dots were varied. The RDK was composed of two surfaces, moving in directions offset by 45° , except for Experiment 7, in which one of the two apertures contained only one surface, the comparison surface. The overall dot density of the RDK was 1 dot/dva^2 , except in Experiment 4 and Experiment 7, in which dot density was varied. The distribution of dots to the two surfaces was varied as independent variable. In Experiment 7, a red bull's eye was presented in between the two RDK apertures at zero disparity. Stimulus presentation was controlled by Matlab, using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997).

Experimental procedure

Observers had to fixate a red bull's eye at the beginning of each trial. By pressing a button, they started the trial and immediately saw the transparent surfaces. After 1 s, the trial ended and observers had to give their perceptual judgment (Figure 1). The required type of judgment differed between the experiments. In Experiment 1, observers had to indicate the motion direction perceived in the back or perceived as more numerous in separate sessions. In Experiment 1, observers were instructed to track the motion with their eyes. In Experiments 2–4 and Experiment 6, observers had to indicate the motion direction perceived as more numerous. In Experiment 5, observers had to indicate the depth layer of the surface which they perceived as more numerous (front or back). In Experiment 7,

observers had to compare the numerosity of the surfaces which appeared in the same depth plane, and to indicate the surface with more dots (left or right). Observers were also asked to fixate the central fixation target.

There is an ongoing debate whether numerosity can be judged independently from density or not (Burr & Ross, 2008; Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Durgin, 2008; Ross & Burr, 2010). In the current experiments, numerosity and density were confounded because the surface area was held constant. Since we asked observers for numerosity judgments, we use this term, but under our conditions numerosity is exchangeable with density.

Eye tracking setup

For Experiment 1, stimuli were displayed on a 21-inch SONY GDM-F520 CRT monitor driven by an Nvidia Quadro NVS 290 graphics board with a refresh rate of 100 Hz noninterlaced. At a viewing distance of 47 cm, the active screen area subtended 45 dva horizontally and 36 dva vertically. With a spatial resolution of 1280×1024 pixels, this resulted in 28 pixels/dva. The luminance of white, gray, and black pixels was 87, 14.6, and 0.04 cd/m^2 , respectively.

Eye position signals of the right eye were recorded with a video-based eye tracker (EyeLink 1000; SR Research, Kanata, Ontario, Canada) and were sampled at 1000 Hz. The eye tracker was driven by the EyeLink toolbox (Cornelissen, Peters, & Palmer, 2002). Eye velocity signals were obtained by digital differentiation of eye position signals over time. The eye position and velocity signals were filtered by a Butterworth filter with cutoff frequencies of 30 and 20 Hz, respectively. Saccade onset and offsets were determined with the EyeLink saccade algorithm. Saccades were removed from the velocity traces by linear interpolation. For each trace, the angular direction of the eye velocity was calculated in 50-ms-wide time intervals centered on 0 to 600 ms after transparent motion onset. Binary eye movement decisions were classified according to which surface direction was closer to the eye movement direction and used to calculate oculometric functions (Kowler & McKee, 1987).

To further analyze the trial-by-trial relation of eye movements and perceptual decisions, we rotated all eye movement traces to the mean direction of the two surface motions and calculated eye velocity in this average direction as well as eye velocity orthogonal to it. The eye velocity in the average direction can be taken as measure of the general eye speed; the eye velocity in the orthogonal direction can be taken as measure of the selectivity for one of the two surfaces. The trials were grouped according to the perceptual judgments choosing the surface moving upward or

downward. To quantify the difference in the orthogonal eye velocity distributions when the upward or the downward moving surface was perceptually selected, the area under the ROC curve was calculated. Additionally, the eye movement gain was calculated for the average direction and the orthogonal direction by dividing eye velocity by the corresponding speed of the perceptually chosen surface motion.

Stereoscope setup

In Experiments 2 to 7, stimuli were displayed on two 19-inch LCD Dell UltraSharp 1907FP monitors driven by a Nvidia Quadro NVS 285 with a refresh rate of 75 Hz. At a viewing distance of 55.5 cm, the active screen area subtended 39 dva horizontally and 31 dva vertically. With a spatial resolution of 1280×1024 pixels, this resulted in 33 pixels/dva². The luminance of white, gray, and black pixels was 97.9, 30.3, and 0 cd/m² (below the sensitivity of a Photo Research PR 650), respectively.

Stimuli for the left eye were presented on the left monitor screen and stimuli for the right eye on the right monitor screen. A Wheatstone mirror stereoscope, consisting of two first surface mirrors (169×194 mm) was used to bring the two views into alignment. Three-dimensional vision was tested prior to the experiments with a Stereo Optical graded circle test and all observers in Experiments 2 to 7 had normal stereo vision. The two surfaces were presented at 7.4 arcmin relative disparity, except for Experiments 2 and 6, which additionally contained a zero disparity condition and Experiment 3, where the relative disparity was 3.7, 11.0, or 25.7 arcmin. In all disparity conditions, one surface was presented in front of the fixation plane and one surface behind the fixation plane, so that the magnitude of disparity was identical for the front and the back surface and the only difference being the sign of disparity.

Psychophysical data analysis

The method of constant stimuli was used in all experiments. The surface difference (N_{Δ}) was calculated as the difference between the number of the dots in the two surfaces (N_1 , N_2) divided by the total number of dots (Equation 1). The surface difference was zero, if both surfaces had the same number of dots; -100% , if all of the dots were in the second surface (N_2); and $+100\%$ if all of the dots were in the first surface (N_1).

$$N_{\Delta} = \frac{(N_1 - N_2)}{(N_1 + N_2)} \quad (1)$$

The surface difference was -60 , -40 , -20 , 0 , 20 , 40 , and 60% except for Experiment 7. Here the standard surface had 64, 114, or 165 dots. The inducing surface had also 64, 114, or 165 dots. The surface difference between the standard and the comparison surface, which had to be compared by the observers, was -30% , -20% , -10% , 0% , 10% , 30% , and 60% . In this experiment, the psychometric functions were fitted to the number of dots in the comparison surface, in all other experiments to the surface difference between the two overlapping surfaces.

Cumulative Gaussian functions were fitted to the data, using the psignifit toolbox (Wichmann & Hill, 2001). The point of subjective equality (PSE) was defined as the mean of the cumulative Gaussian function. The just noticeable difference (JND) was defined as the standard deviation of the cumulative Gaussian function. Since we could not fit psychometric functions to all conditions in Experiment 1, we used a different analysis for this experiment. Here we used the proportion of backward choices and more numerous choices at a surface difference of zero. These proportions were arcsine-square-root transformed before they were submitted to statistical procedures. All p values in ANOVAs are reported with Greenhouse–Geisser correction.

To quantify the magnitude of the directional biases in Experiments 1, 2, and 6, we calculated the root mean square error (RMSE) of the PSEs relative to the average PSE across all directions. The RMSE is zero, if the PSEs are identical for all directions and 100% , if PSEs are maximally different for all directions. For the proportion of choices in Experiment 1 the RMSE ranges from 0% to 50% .

To quantify the influence of the numerosity of the inducing surface (N_I) on the perceived numerosity of the standard surface (N_S) in Experiment 7, we fitted a model, which adds or subtracts a proportion (a) of the dots in the inducing surface to the dots in the standard surface (Equation 2).

$$N_C = N_S + aN_I \quad (2)$$

Separate parameters a were determined for the two conditions in which the standard surface was in the front or in the back.

Results

Direction biases for perception of depth order and numerosity (Experiment 1)

In Experiment 1, we measured the directional biases of depth order judgments, numerosity judgments, and smooth pursuit eye movements. Previous studies

showed that certain motion directions are more likely to be perceived in the back (Mamassian & Wallace, 2010; Schütz, 2011) and that there is a bias to see the motion with more dots in the back (Schütz, 2011). Hence we asked if perceived numerosity is influenced by motion direction and perceived depth order.

Across observers proportion of choices for numerosity and depth order judgments were significantly different for different motion directions, $F(7, 77) = 4.18$, $p = 0.020$. There was no difference between depth order and numerosity, $F(1, 11) = 3.22$, $p = 0.10$, no significant interaction between motion direction and perceptual task, $F(7, 77) = 2.17$, $p = 0.10$. This means that there were significant anisotropies for both, depth order, and numerosity judgments (Figure 2A). For depth order judgments three direction pairs showed significant biases: leftward motion was always seen behind motion down-left, M 100%, SD 0.0, which in turn was seen more often in the back than downward motion, M 89.3%, SD 21.6, $t(11) = 3.24$, $p = 0.008$, and upward motion was seen less often in the back than motion up-left, M 14.2%, SD 26.4, $t(11) = -2.57$, $p = 0.026$. There were no significant biases for the other direction pairs (all $p > 0.261$). For numerosity judgments, leftward motion was consistently seen as more numerous than motion down-left, M 90.9%, SD 7.8, $t(11) = -5.85$, $p < 0.001$, and upward motion was seen as less numerous than motion up-left, M 17.3%, SD 23.7, $t(11) = -2.43$, $p = 0.034$. There were no significant biases for the other direction pairs (all $p > 0.070$).

The fact, that there were on average only weak anisotropies across observers leaves the possibility that individual observers showed stronger anisotropies which were not aligned across directions. In order to quantify the magnitude of directional biases for individual observers and for the average across observers, we calculated the RMSE of the proportion of choices relative to the average proportion of choices across all directions (Figure 2B). For the proportion data the RMSE can vary between 0% and 50%. The RMSE of the anisotropies averaged across all observers (Figure 2A) was 24.5% for depth order judgments and 17.9% for numerosity judgments. Next we calculated the RMSE for each observer individually. For depth order judgments, the RMSE was 45.3% (SD 5.0) and significantly larger than the population value of 24.5%, $t(11) = 14.26$, $p < 0.001$. For numerosity judgments the RMSE was 36.6% (SD 9.7) and also significantly larger than the population value of 17.9%, $t(11) = 6.66$, $p < 0.001$. The RMSE was significantly larger for depth order judgments than for numerosity judgments, $t(11) = -2.98$, $p = 0.013$. These results provide evidence for anisotropies in perceived depth order and perceived numerosity. There were interindividual differences in anisotropies, because the individual anisotropies were larger than the population anisotropies averaged across observers. Interestingly, the magnitude of anisotropies was larger for perceived depth order than for perceived numerosity. This suggests that motion direction had a stronger and more direct influence on perceived depth order than on perceived numerosity.

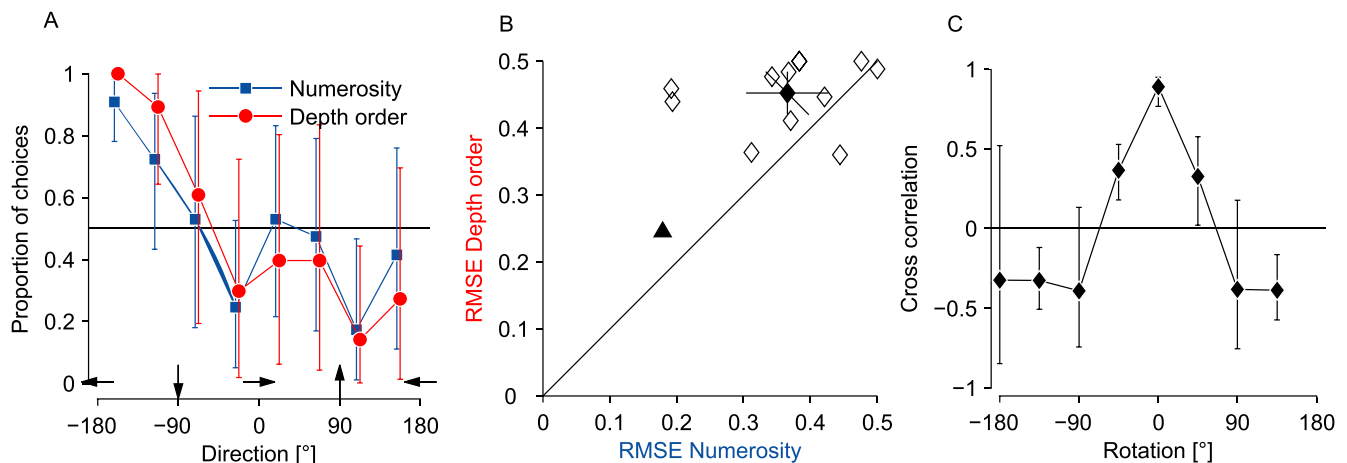


Figure 2. Experiment 1. Anisotropies of perceived depth order and perceived numerosity. (A) Proportion of choices for depth order (red) and numerosity (blue) judgments over motion directions. The values for depth order and numerosity are horizontally offset to improve the visibility. The black arrows illustrate motion directions. (B) RMSE of anisotropies for depth order and numerosity judgments. Open diamonds represent individual observers, the filled diamond the average RMSE across observers. The filled triangle represents the RMSE of the average anisotropies across observers from Figure 2A. (C) Circular cross correlation between anisotropies for perceived depth order and perceived numerosity. The x-axis denotes the direction rotation between depth order and numerosity values. (A–C) Error bars indicate 95% confidence intervals.

Since both depth order and numerosity showed anisotropies, it is an obvious question whether they share the same anisotropies. The average anisotropies across observers were very similar for depth order and numerosity judgments (Figure 2A). To investigate whether this was also the case for individual observers, we calculated for each observer a circular cross correlation between the proportion of choices for depth order and numerosity judgments (Figure 2C). Across observers, the cross correlation had a clear maximum of 0.89 at 0° offset between the preferences for numerosity and depth order and only rotations of 45° clockwise or counterclockwise were also significantly larger than zero. These results indicate that the anisotropies for depth order and numerosity judgments were aligned also for individual observers. Directions that were more likely to be seen in the back were also more likely to be seen as more numerous.

Direction biases of smooth pursuit eye movements (Experiment 1)

To investigate the relation of perception and eye movements, we recorded smooth pursuit eye movements in the same sessions of Experiment 1 and calculated the directional preferences. Two hundred milliseconds after motion onset (Figure 3A), average eye movement anisotropies were in general weak and differed between numerosity and depth order conditions. Six hundred milliseconds after motion onset (Figure 3B), these anisotropies were more pronounced and also more similar to each other and to the perceptual anisotropies.

To quantify the magnitude of anisotropies, we calculated the RMSE of the proportion of eye movement choices relative to the proportion across directions, just like for the psychophysical data (Figure 3C). The RMSE started at a value of about 20% and then gradually increased over time, $F(12, 132) = 11.00$, $p < 0.001$. There was also a significant effect of perceptual conditions, $F(1, 11) = 9.69$, $p = 0.01$, and a significant interaction between time and perceptual condition, $F(12, 132) = 2.73$, $p < 0.034$. Hence the anisotropies in eye movements were not identical in the two perceptual conditions. In the condition with depth order judgments, the RMSE saturated after 250 ms at a value of about 32%. In the condition with numerosity judgments, the RMSE reached a constant level after 250 ms at a value of about 28%. In both depth order and numerosity conditions, the RMSEs were smaller for pursuit than for perception. This could be taken as evidence that the direction biases were caused initially by perception and then were transferred to the eye movements.

Although the magnitude of anisotropies was smaller for eye movements than for perception, it is possible that they share the same anisotropies. To quantify this, we calculated a circular cross correlation between eye movements and the perceptual judgments (Figure 3D). Here we analyzed only the correlations at a 0° rotation. These correlations increased over time, $F(12, 132) = 18.54$, $p < 0.001$, and they differed between the two perceptual conditions, $F(1, 11) = 13.77$, $p = 0.003$. There was also a significant interaction between time and perceptual condition, $F(12, 132) = 2.91$, $p = 0.039$. For depth order judgments, this correlation was significantly larger than zero from 150 ms after motion onset and reached a maximum value of 0.89. For numerosity judgments, this correlation was significantly larger than zero from 200 ms after motion onset and reached a maximum value of 0.68. Hence the anisotropies of eye movements were very similar to the perceptual anisotropies after a short period of time.

The analysis of anisotropies only detects average biases across trials. Here we further investigated the trial-by-trial variations of eye movements and perceptual decisions. We calculated the eye movement gain separately in the average direction of the two surface motions and orthogonal to the average direction, in the direction of the surface motion that was selected by the observer in the same trial. The eye movement gain in the average direction is a measure of the general speed of the eye movements. The eye movement gain in the orthogonal direction is a measure of surface selection (Figure 4A). In general, the eye movement gain increased over time, $F(12, 132) = 153.10$, $p < 0.001$. Furthermore it was lower in the numerosity than in the depth order condition, $F(1, 11) = 18.45$, $p = 0.001$, and lower in the orthogonal than in the average direction, $F(1, 11) = 58.73$, $p < 0.001$. In the average direction, eye movement gain exceeded zero 100 ms after motion onset, in both perceptual conditions. In the orthogonal direction, eye movement gain rose later, 150 ms after motion onset in the depth order condition and 200 ms after motion onset in the numerosity condition. These results show that the eyes moved initially mainly in the average direction of the surfaces and only later moved in the direction of the perceptually relevant surface. This selectivity appeared earlier in the depth order than in the numerosity condition. The eye movement gain in the average direction saturated at a value of 0.85 in the depth order condition and a value of 0.79 in the numerosity condition. In the orthogonal direction eye movement gains reached only 0.58 in the depth order condition and 0.30 in the numerosity condition. This means that the perceptual decision was more closely related to the eye movements in the depth order than in the numerosity condition.

In a supplementary analysis we calculated the area under a ROC curve based on the eye velocity

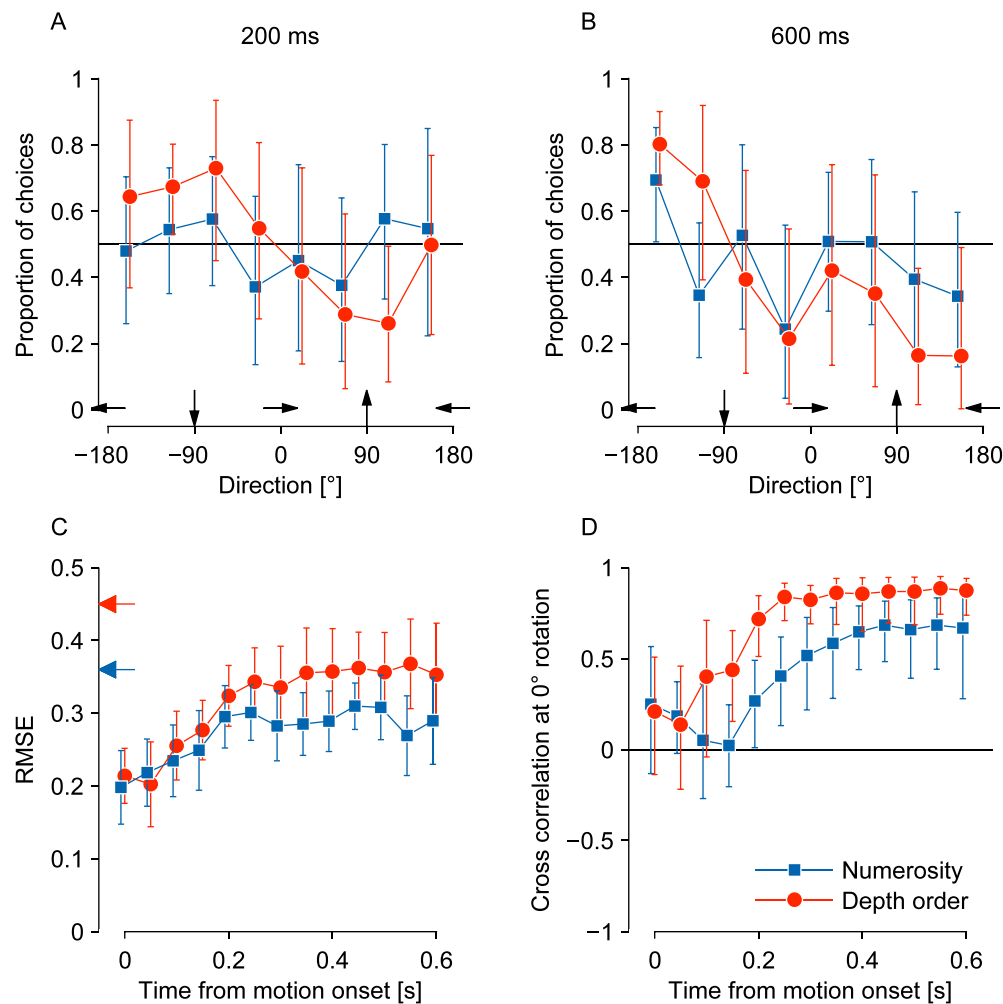


Figure 3. Experiment 1. Anisotropies of smooth pursuit eye movements. (A) Proportion of eye movement choices 200 ms after motion onset. (B) Proportion of eye movement choices 600 ms after motion onset. (A, B) Conventions are the same as in Figure 2A. (C) RMSE of anisotropies for smooth pursuit eye movements in the two perceptual conditions. The arrows indicate the average perceptual RMSE in these conditions taken from Figure 2B. (D) Circular cross correlation for a 0° direction rotation between perception and eye movement data. (A–D) Values for numerosity and depth order conditions are plotted in blue and red respectively. Error bars indicate 95% confidence intervals.

distributions in the orthogonal direction, when the surface moving upward or downward was selected (Figure 4B). The results for this analysis were very similar to the correlation analysis of the anisotropies (Figure 3D). ROC values increased over time, $F(12, 132) = 58.87$, $p < 0.001$, and were significantly lower in the numerosity condition than in the depth order condition, $F(1, 11) = 14.78$, $p = 0.003$. Furthermore this difference changed over time, $F(12, 132) = 6.17$, $p = 0.001$. In the depth order condition ROC values were significantly larger than 0.5 from 150 ms on and saturated at a value of 0.89. In the numerosity condition ROC values were significantly larger than 0.5 from 200 ms on and saturated at a value of 0.75.

Taken together, the cross-correlation between eye movement and perceptual anisotropies and the trial-by-trial correlation of eye movements and perceptual

decisions rose slower and saturated at a lower level for the numerosity condition than for the depth order condition. This suggests that the direction biases in perceived numerosity were merely a consequence of the direction biases in perceived depth order. This hypothesis is tested in the next experiments.

Effect of disparity

Experiment 2

Experiment 1 showed that depth order and numerosity judgments shared the same directional biases. However this establishes only a correlative, but not a causal relationship. In order to investigate, if depth order causally influences perceived numerosity, we presented the two surfaces in two disparity conditions,

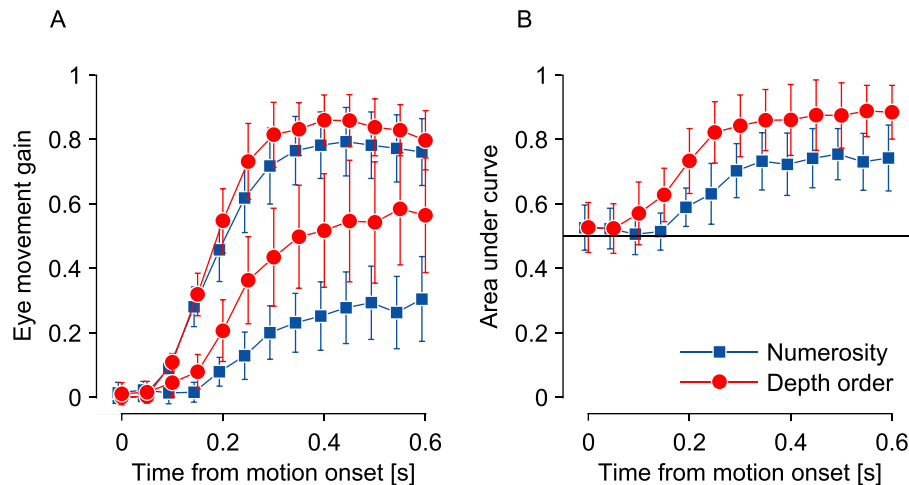


Figure 4. Experiment 1. Trial by trial correlation of eye movements and perceptual decisions. (A) Eye movement gain in the average direction of the two surface directions (two upper traces) and orthogonal to the average direction, in the direction of the perceptually selected surface motion (two lower traces). (B) Area under the ROC curve based on the eye movement velocity orthogonal to the average direction. (A,B) Values for numerosity and depth order conditions are plotted in blue and red respectively and are horizontally offset to improve the visibility. Error bars indicate 95% confidence intervals.

either at zero or at 7.4 arcmin relative disparity. Separate PSEs were calculated for each combination of motion directions and disparity condition (Figure 5A). There were significant main effects for motion direction, $F(7, 70) = 3.29$, $p = 0.030$, and disparity, $F(1, 10) = 15.89$, $p = 0.003$, and also a significant interaction between the two factors, $F(7, 70) = 3.15$, $p = 0.035$. In the disparity condition, the perceived numerosity of the two surfaces was equal, if the back surface had 11.0% ($SD 7.8$) fewer dots, $t(10) = -4.63$, $p = 0.001$. Hence there was a bias to see more dots in the back surface than in the front surface. In the no-disparity condition,

there average PSE ($M -1.0\%$, $SD 2.9$) across motion directions was not significantly different from zero, $t(10) = -1.10$, $p = 0.296$. This shows that there was no constant bias across directions in the no-disparity condition, but that the back surface was seen as more numerous across directions in the disparity condition. Hence disparity or depth order exhibited a causal influence on numerosity judgments.

To quantify the effect of motion direction, we calculated the RMSE of the PSEs relative to the average PSE across all directions (Figure 5B). For the PSEs the RMSE can vary between 0% and 100%. In

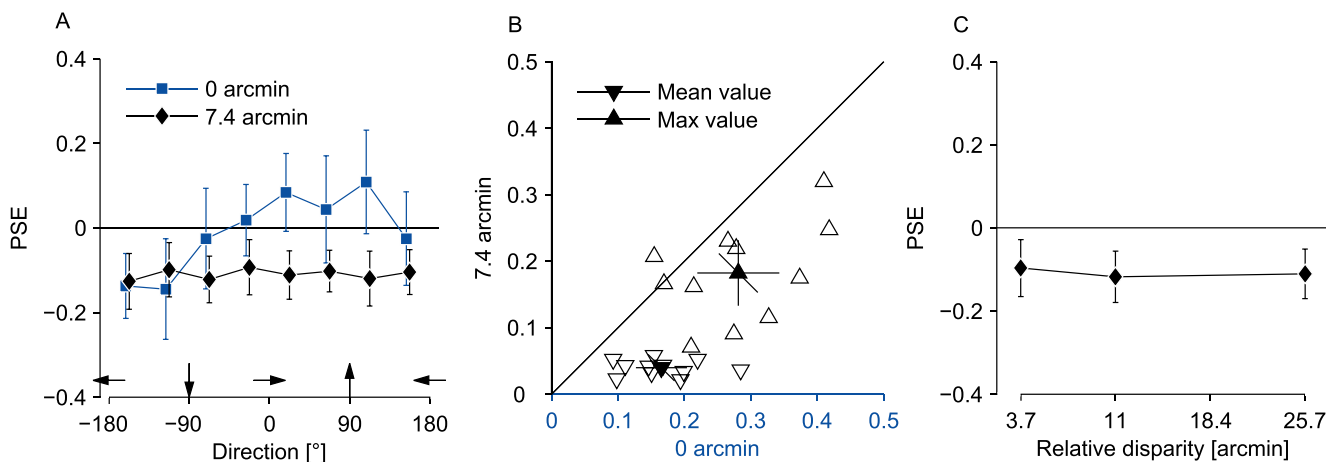


Figure 5. Effects of disparity on perceived numerosity. (A) PSE over direction. The 7.4 and 0 arcmin conditions are plotted in black and blue, respectively. The values for 7.4 and 0 arcmin are horizontally offset to improve the visibility. (B) Average deviations from the mean across directions and maximum absolute PSEs are plotted with downward and upward pointing triangles, respectively. (A, B) Experiment 2. (C) Experiment 3. PSE over relative disparity. (A–C) Open symbols represent individual observers, closed symbols the average across observers. Error bars indicate 95% confidence intervals.

the no-disparity condition, this value was on average 16.6% (SD 5.7) and significantly larger than zero, $t(10) = 9.61$, $p < 0.001$. In the disparity condition, this value was on average 4.0% (SD 1.2) and significantly larger than zero, $t(10) = 11.23$, $p < 0.001$. The value in the disparity condition was significantly smaller than in the no-disparity condition, $t(10) = 7.08$, $p < 0.001$.

There was no influence of disparity or motion direction on the JNDs. Across observers and conditions, the average JND of the psychometric functions was 12.2% (SD 4.3). Hence the effect of motion direction in the disparity condition was about a third of a JND and thus is negligible. These results suggest that the presence of disparity abolishes the influence of motion direction on numerosity judgments almost completely. However, the numerosity bias in the disparity condition was pretty large, since it was about one JND.

To quantify the maximal bias imposed either by disparity or by motion direction, we compared the maximum absolute PSEs (Figure 5B). In the no-disparity condition, this value was 28.1% (SD 9.2) and significantly larger, $t(10) = 3.76$, $p = 0.004$, than the value of 18.2% (SD 7.3) in the disparity condition. These results suggest that the biases due to motion direction in the no-disparity case can exceed the bias induced by a relative disparity of 7.4 arcmin.

Experiment 3

Experiment 2 indicated that the numerosity of the back surface was overestimated. However it is not clear whether the overestimation depends on the magnitude of relative disparity or only on the depth order. To distinguish these alternatives, we varied the relative disparity in three steps (Figure 5C). The perceived numerosity of the two surfaces was equal, if the back surface had 9.6%, 11.8%, and 11.1% fewer dots for relative disparities of 3.7, 11.0, and 25.7 arcmin, respectively. Since there was no significant effect of the magnitude of relative disparity, $F(2,20) = 0.97$, $p = 0.37$, the perceived numerosity depended solely on depth order.

The results of Experiments 2 and 3 indicate that the perceived depth order imposed a bias on the perceived numerosity, so that more dots were perceived in the back than in the front surface. Hereby perceived depth order could be induced by directional biases or by disparity.

Stability of direction biases for perceived numerosity (Experiments 1 and 2)

Eleven observers participated in Experiments 1 and 2, so that we can compare the anisotropies for

numerosity in these two experiments. The circular cross correlation had a significant peak of 0.69 (SD 0.52) at a rotation of 0° , $t(10) = 4.90$, $p = 0.001$. These data were collected on different setups, with an average pause of 90 days (SD 52, minimum 6 days, maximum 187 days) and the length of the pause did not affect the magnitude of correlations, $r = 0.11$, $p = 0.758$. This suggests that the anisotropies in perceived numerosity were at least as robust as the anisotropies in perceived depth order, which have been shown to be stable over two weeks (Mamassian & Wallace, 2010).

Effect of uncertainty

Experiment 4

One possible explanation for the misperception of numerosity in the front and back surfaces is that crowding makes it difficult to identify single dots and correctly assign them to the two surfaces (Whitney & Levi, 2011; Wu et al., 2004). In this case, the magnitude of the bias should be smaller for more sparse fields. To test this hypothesis we varied the overall field density in four steps from 0.25 dots/dva² (79 dots) to 2 dots/dva² (628 dots). As in the previous experiments, the numerosities of the surfaces appeared as equal, if a smaller percentage of dots was in the back surface (Figure 6A): the average PSEs were 14.2%, 11.7%, 11.4%, and 10.9% for field densities of 0.25, 0.5, 1.0, and 2.0 dots/dva². These values were not significantly different from each other, $F(3,30) = 1.00$, $p = 0.388$. Although a display with 0.25 dots/dva² is certainly still crowded, one would expect a smaller bias than in a display with 2 dots/dva² if crowding causes the numerosity bias. Further evidence against a crowding explanation comes from the distribution of the JNDs, which decreased from 19.3% at 0.25 dots/dva² to 13.7% at 2 dots/dva². Hence reducing the field density made the task more difficult and not easier, $F(3,30) = 3.97$, $p = 0.027$, also incompatible with the hypothesis that crowding impaired performance due to the field density. The JND results are consistent with findings from stereoscopic transparency, which show that signal thresholds decrease with increases of dot density for dot densities below about 2 dots/dva² (Wallace & Mamassian, 2004).

Experiment 5

Another potential reason for the numerosity bias is the difficulty to attend the moving dots, given their relatively fast speed of 10 dva/s and their short lifetime of 200 ms. To test this hypothesis we varied the speed of the dots (0, 5, and 10 dva/s) and compared conditions with an unlimited lifetime or 200 ms limited lifetime (Figure 6B). Across all conditions, the surface in the back appeared more numerous. The dot lifetime

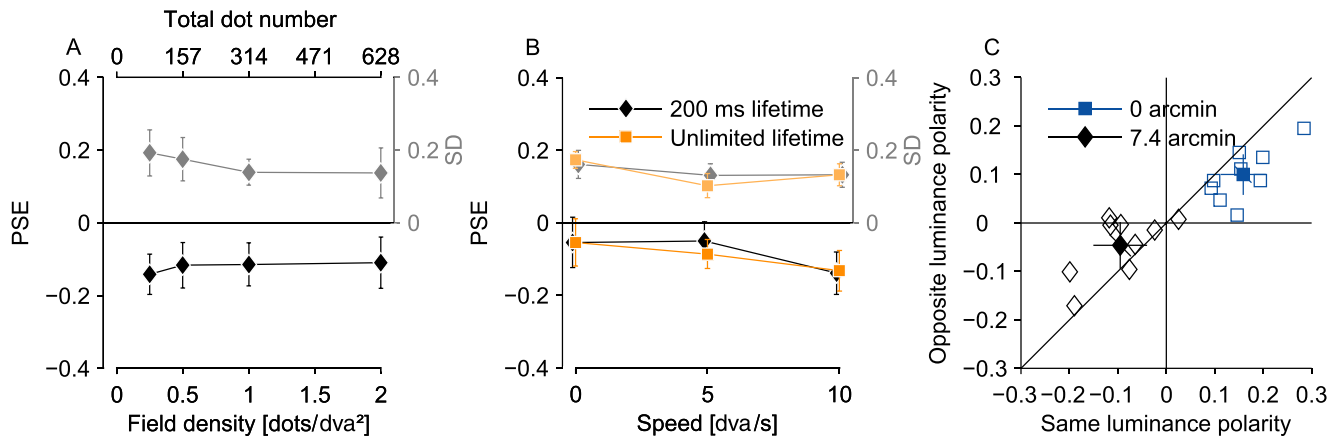


Figure 6. Effects of uncertainty. (A) Experiment 4. PSE (black) and *SD* (gray) over field density. (B) Experiment 5. PSE (dark colors) and *SD* (light colors) over motion speed. Limited (200 ms) and unlimited lifetime are plotted in black and orange respectively and are horizontally offset to improve the visibility. (C) Experiment 6. RMSE of anisotropies in the zero arcmin condition (blue). Average PSEs across directions for the 7.4 arcmin condition (black). Open symbols represent individual observers, closed symbols the average across observers. (A–C) Error bars indicate 95% confidence intervals.

had no significant effect, $F(1, 9) = 1.02$, $p = 0.340$, indicating that the numerosity bias was not caused by missassignment of disappearing and reappearing dots. The dot speed, however, influenced the numerosity bias significantly, $F(2, 18) = 5.45$, $p = 0.041$, and the numerosity biases were only significant at 5 dva/s, $M -6.8\%$, $SD 6.0$, $t(9) = -3.69$, $p = 0.006$, and 10 dva/s, $M -13.5\%$, $SD 7.9$, $t(9) = -5.45$, $p < 0.001$, but not at 0 dva/s, $M -5.4$, $SD 9.0$, $t(9) = -1.90$, $p = 0.090$. These results suggest that the numerosity bias was at least partially driven by motion. To investigate how dot lifetime and dot speed affected the difficulty of the task, we analyzed the JNDs. The dot lifetime had no significant effect on JNDs, $F(1, 9) = 0.18$, $p = 0.679$. Dot speed influenced the JNDs significantly, $F(2, 18) = 7.62$, $p = 0.011$, with JNDs of 16.7% ($SD 3.7$), 11.7% ($SD 2.6$), and 13.3% ($SD 3.8$) at 0, 5, and 10 dva/s respectively. This means that the task was equally difficult for limited and unlimited dot lifetime, but more difficult for stationary dots than for moving dots.

Experiment 6

Finally, we investigated whether the direction and numerosity biases can be attenuated, if the two surfaces can be distinguished by another feature, in addition to motion direction and disparity. To this end, we presented the surfaces at opposite luminance polarities. As in Experiment 2, we had two disparity conditions (0 and 7.4 arcmin). By directly comparing Experiment 2, which had identical luminance polarities and Experiment 6, we can measure the influence of luminance polarity (Figure 6C). Nine observers participated in both experiments. For the condition without disparity, we calculated the RMSE of the PSEs relative to the average PSE across all directions. The RMSE was

significantly smaller, $t(8) = 4.09$, $p = 0.003$, for opposite luminance polarity ($M 10.0\%$, $SD 5.4$) than for the identical luminance polarity ($M 15.9\%$, $SD 6.1\%$). Hence the addition of a luminance difference between the surfaces reduced the directional biases. For the condition with disparity, we calculated the average PSE across all directions. Also here the PSEs were significantly smaller, $t(8) = -2.50$, $p = 0.037$, for opposite luminance polarity ($M -4.7\%$, $SD 6.3$) than for identical luminance polarity ($M -9.5\%$, $SD 7.2$). This means that the luminance cue also reduced the bias to see more dots in the surface in the back.

To investigate whether the luminance cue reduced only the biases or whether it also facilitated the perceptual task per se, we additionally analyzed the JNDs. In the condition without disparity, there was no significant difference, $t(8) = 1.25$, $p = 0.248$, between the experiment with opposite luminance polarity ($M 10.3\%$, $SD 5.9$) and the experiment with identical luminance polarity ($M 11.7\%$, $SD 5.0$). Also in the condition with disparity, the JNDs did not differ, $t(8) = 1.93$, $p = 0.09$, between the experiment with opposite luminance polarity, $M 10.5\%$, $SD 3.9$, and the experiment with identical luminance polarity, $M 12.5\%$, $SD 3.9$. These results show that the luminance cue reduced the bias, without facilitating the task itself. Hence it is very unlikely that the observers used completely different perceptual strategies in these two experiments.

Overestimation in the back versus underestimation in the front (Experiment 7)

In the previous experiments, observers had to compare the numerosity of the two overlapping

surfaces with each other, so that we don't know if numerosity in the back was overestimated or numerosity in the front was underestimated. To distinguish between these possibilities, we presented a single surface neighboring the overlapping surfaces. The single surface was either aligned in depth with the front or the back surface and its numerosity was varied. Observers had to judge if either the single surface or the overlapping surface in the same depth plane was more numerous (Figure 7A). The numerosity of each of the overlapping surfaces could be 64, 114, or 165, corresponding to field densities of 0.25, 0.45, and 0.65 dots/dva² dots.

When the single surface was aligned in depth with the back surface, the PSE increased with increasing numerosity of the front surface (Figure 7B). For instance, to match a back surface of 114 dots, about 125 or 157 dots were needed in the single surface, when the front surface had 64 or 165 dots, respectively. This indicates that the numerosity in the back was overestimated by a certain proportion of the numerosity in the front. When the single surface was aligned in depth with the front surface, the PSE decreased with increasing numerosity of the back surface. For instance, to match a front surface of 114 dots, only about 107 or 97 dots were needed, when the back surface had 64 or 165 dots, respectively. This indicates

that the numerosity in the front was underestimated by a certain proportion of the numerosity in the back.

The statistical analysis showed significant main effects of the standard surface, $F(2, 18) = 526.39$, $p < 0.001$, of the inducing surface, $F(2, 18) = 6.20$, $p = 0.016$, and of disparity condition (front vs. back), $F(1, 9) = 40.55$, $p < 0.001$. The effect of the inducing surface depended on the standard surface, as shown by a significant two-way interaction between standard and inducing surface, $F(4, 36) = 3.34$, $p = 0.037$. The effect of the inducing surface also depended on the disparity condition, as shown by a significant two-way interaction, $F(2, 18) = 42.49$, $p < 0.001$.

To shed more light on the specific interactions, we fitted the data by a simple linear model, which adds or subtracts a certain proportion of the dots from the inducing surface to the standard surface (Equation 2). The model contained two free parameters, one each for the condition where the standard surface was in front or in the back (Figure 7C). With just two free parameters the model explained on average 94.7% (SD 2.7%) of the variance. The model parameters showed that on average 21.9% (SD 13.6%) of the dots in the front surface were added to the back surface, $t(9) = 5.06$, $p = 0.001$, if the standard surface was in the back. On average 10.7% of the dots in the back surface were missing in the front surface, $t(9) = 2.87$, $p = 0.018$, if the standard surface was in the front. Although these

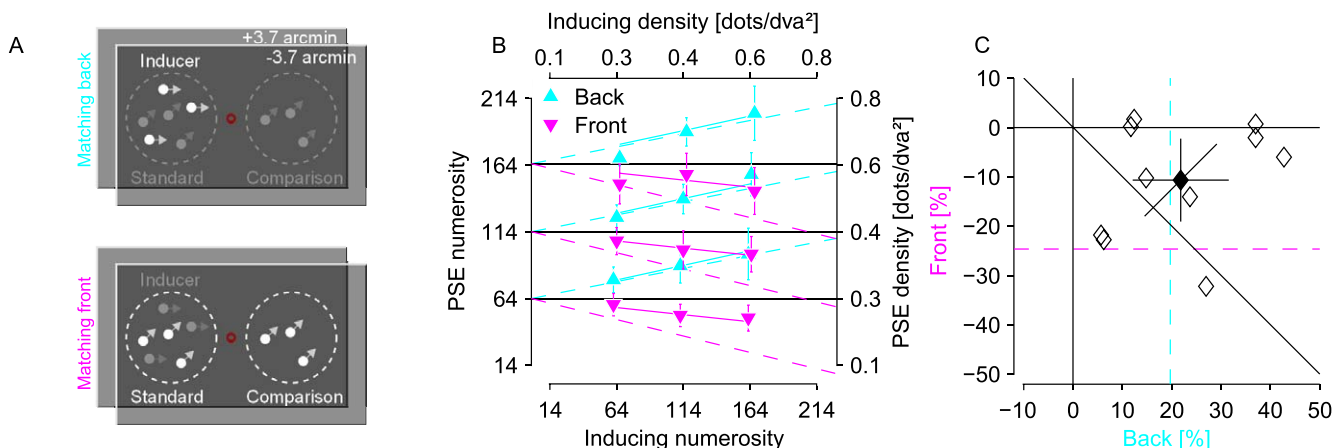


Figure 7. Experiment 7. Effects at the front versus back surface. (A) Experimental paradigm. Observers had to judge which of the two surfaces, lying in the same depth plane, is more numerous (left or right). The comparison surface was always in the same depth plane as the standard surface. The standard surface could be in the back (cyan) or in the front (magenta). In between the two apertures, a red bull's eye was presented as fixation target at zero disparity. Stimuli are not drawn to scale and the labels and the dashed circles were not part of the display. (B) PSE over inducing dot number. The solid lines represent the fitted model. The horizontal lines represent the numerosity of the standard surface, which was either in the back (cyan) or in the front (magenta). If the inducing surface has no influence, all values should lie on the horizontal lines. The dashed lines show predictions under the assumption that the effect in Experiment 2 (Figure 5A) is only based on an overestimation of the surface in the back (cyan) or on an underestimation of the surface in the front (magenta). The values for the different standard numerosities are horizontally offset to improve the visibility. (C) Slope of fitted model. The slope indicates how many of the inducing dots have to be added or subtracted to the standard dots. Open symbols represent individual observers, closed symbols the average across observers. The dashed lines correspond to the predictions in B. (B, C) Error bars indicate 95% confidence intervals.

values were not significantly different from each other, $t(9) = 1.73$, $p = 0.118$, they were not correlated across observers ($r = -0.29$, $p = 0.41$). Interestingly, there were different result patterns for different observers. Five observers did not underestimate the front surface, two observers did not overestimate the back surface, and three observers had effects on the front and the back surface. These results show that the numerosity of the back surface was overestimated and the numerosity of the front surface was underestimated at the same time.

Based on the average effect size in the disparity condition from Experiment 2, we can predict effects for the present experiment under the assumption that either numerosity is solely overestimated in the back or solely underestimated in the front. The average numerosity difference of 11.0% in Experiment 2 could be obtained if numerosity in the back is overestimated by 19.8% of the dots in the front or if numerosity in the front is underestimated by 24.7% of the dots in the back. In the present experiment, the numerosity in the back was overestimated by 21.9% and the numerosity in the front was underestimated by 10.7%. Thus the overestimation in the back could fully account for the effects in Experiment 2, $t(9) = 0.52$, $p = 0.618$, whereas the underestimation in the front was too small to account for these effects, $t(9) = 2.37$, $p = 0.04$. Although there was both an overestimation in the back and an underestimation in the front, most of the relative effect seemed to originate from the overestimation in the back.

Cognitive theories proposed that numbers are represented in a spatial coordinate system with small numbers associated with left and large numbers associated with right (Dehaene, Dehaene-Lambertz, & Cohen, 1998; Walsh, 2003). We did not find any evidence for such a spatial association in our data because there were no consistent differences between a comparison surface presented on the left or on the right.

Discussion

In a series of experiments we investigated interactions between perceived depth order and perceived numerosity. In the absence of disparity differences, anisotropies of perceived depth order and perceived numerosity were highly correlated: directions which were more likely to be perceived in the back were also more likely to be perceived as more numerous (Experiment 1). The magnitude of anisotropies was larger for depth order than for numerosity, suggesting a closer link between motion direction and depth order than between motion direction and numerosity. Smooth pursuit eye movements showed similar anisot-

ropies as perception, with increasing correlations between eye movements and perception over time. The pursuit anisotropies were correlated earlier with depth order biases than with numerosity biases, indicating that depth order was processed before numerosity. The magnitude of anisotropies for eye movements also increased over time, but never reached the same level as the perceptual anisotropies. This could be interpreted as evidence that the origin of the anisotropies was perceptual and the anisotropies in eye movements merely a consequence. Interestingly, the anisotropies for perceived numerosity were remarkably stable over several weeks (Experiment 1 and 2), similar to the stable anisotropies of depth order (Mamassian & Wallace, 2010).

When the surfaces were presented at different disparities, the anisotropies of perceived numerosity vanished and the surface in the back was consistently perceived as more numerous (Experiment 2). This numerosity bias depended only on the depth order, but not on the magnitude of disparity (Experiment 3) and was also not consistently affected by the overall field density (Experiment 4) or dot lifetime (Experiment 5). However it was attenuated, when the speed of motion was reduced (Experiment 5) or when the two surfaces differed in their luminance polarity (Experiment 6). The numerosity in the back was overestimated and the numerosity in the front was underestimated, but the overestimation in the back seemed to contribute more to the overall effect (Experiment 7). These results clearly show that perceived numerosity is affected by perceived depth order.

In most of the experiments, the two surfaces were distinguished by motion direction and by disparity. Hence it is quite astonishing, that such large numerosity biases occurred, although two cues were available to segment the surfaces. Only the addition of a further cue, luminance polarity, reduced the bias to a negligible amount (Experiment 6). This suggests that the assignment of single elements to the two surfaces was far from being perfect. The numerosity of the surfaces was probably not computed on a local but on a global scale and only after the surfaces have been segmented.

In the present disparity experiments, dots in one surface were always defined by a common depth and the motion was always fronto-parallel. However, surfaces can also be tilted in depth and defined by a common disparity gradient. Such slanted planes can organize apparent motion (He & Nakayama, 1994) and the spread of spatial attention (He & Nakayama, 1995). It would be interesting to see whether the numerosity biases we observed for fronto-parallel surfaces and motion also occur for slanted surfaces and motion in depth.

Potential causes of the numerosity bias

The presented data show clearly that depth order strongly affects perceived numerosity. A remaining question is how this numerosity bias is created. Here we want to discuss four potential causes. Texture gradient is an important depth cue (Gibson, 1950) and might also have been used in our stimuli. However two properties of our results argue against an interpretation based on texture gradient. First, the magnitude of relative disparity of the surfaces, i.e., their distance in depth did not affect the numerosity bias, only the depth order mattered. The texture gradient however should clearly depend on distance in depth. Second, the numerosity bias had the wrong direction. Consider two surfaces with equal number of dots, but different disparities. Since their retinal density is equal, but they are perceived at different distances, the actual density of the surface in the back has to be lower than the density of the surface in front. In our case, however, the surface in the back was perceived as more numerous, consequently denser. Hence, it is more likely that the texture gradient had no effect or worked against the observed numerosity bias.

The overestimation of numerosity in the back surface might also be consistent with recently published experimental results and predictions of a model of numerosity perception (Dakin et al., 2011). These data show that perceived numerosity and density increase with patch size. Since the retinal size of our surfaces was equal, the surface in the back presumably was perceived as being larger. However, our results indicate that the numerosity bias was probably not caused by a misperception of surface area, because of three reasons. First, the bias also appeared in the standard transparent motion display with zero disparity. It is unlikely that the perceived surface area was affected much by the ambiguous depth order under these conditions. Second, in the last experiment, the matching surface was located in the same depth plane as the standard surface, so that the perceived surface areas should match. Third, the numerosity was not only overestimated in the back, it was also underestimated in the front. Because of these reasons the numerosity bias was presumably not caused by differences in the perceived area of the surfaces.

In pseudotransparent surfaces, elements in the front surface can occlude elements in the back. If the visual system represents actual numerosity, it should compensate these effects of occlusion. In this view the overestimation of numerosity in the back could be interpreted as an overcompensation of occlusion. However this hypothesis is not fully supported by our data. First, the magnitude of overestimation did not depend on the numerosity of the surface in the back (Experiment 7), although the likelihood of occlusion

will be smaller for more sparse fields. Second, it is not clear why a compensation of occlusion should lead to an underestimation of numerosity in the front surface (Experiment 7).

Recently a similar bias has been observed in stereoscopic transparency, using displays with much higher dot density and unlimited presentation duration (Tsirlin, Allison, & Wilcox, 2012). This study showed that the front surface had to be denser in order to be perceived as dense as the back surface. Hence the overestimation of numerosity or density of the back surface seems to be robust with respect to large variations in stimulus properties. Tsirlin et al. (2012) interpreted their results as a consequence of figure-ground segmentation, in which the empty spaces between the dots are automatically assigned to the back surface, which is seen as the background. They modeled this effect by inhibitory connections in a population of neurons tuned to different disparities and an excitatory top-down signal to the depth layer, which is representing the ground. As a consequence of this excitatory top-down signal to the ground layer and its inhibitory connections to the other layers, numerosity is overestimated in the ground layer. The present results are in general consistent with this interpretation and extend the previous results by showing that disparity differences are actually not necessary. Merely the perceived depth order in transparent motion is sufficient to elicit the numerosity bias. This means that the top-down signal for the figure-ground segmentation can be driven by different signals like disparity or motion direction.

The role eye movements

The direction of eye movements showed very similar anisotropies as depth order and numerosity judgments. Also there was a strong trial-by-trial correlation of eye velocities and perceptual decisions in depth order and numerosity judgments. Hence, it is unclear whether the eye movements created the perceptual anisotropies or vice versa. We think that some parts of our data suggest that the perceptual biases were driving the eye movements. First, the magnitude of eye movement anisotropies was smaller than the perceptual anisotropies at any time during the trial (Experiment 1). Second, the eyes moved initially in the average of the two surface directions and became selective for one of the two surfaces 50 (depth order) to 100 (numerosity) ms later (Experiment 1). Third, the numerosity bias was also present when the observers viewed two peripheral apertures and were asked to fixate a central fixation spot (Experiment 7). This indicates that eye movements were not necessary to create the numerosity bias.

Neural substrates

The current experiments were not designed to differentiate between different processing states of numerosity and density. Hence, it might be that the effect is based on texture density. Neurons in the primary visual cortex are selective for spatial frequencies (De Valois & De Valois, 1988) and thus should also respond selectively to different dot densities. Alternatively it might be that the effect is based on numerosity. In the last couple of years, the neural representation of numbers has been studied intensively (for reviews see Nieder, 2005; Piazza & Izard, 2009). It has been shown that neurons in the lateral intraparietal area (LIP) in monkeys (Roitman, Brannon, & Platt, 2007) and in its homologue in humans (Santens, Roggeman, Fias, & Verguts, 2010) encode the numerosity of elements in their receptive fields. Furthermore, a computational neural model that extracts numerosity has been put forward (Stoianov & Zorzi, 2012). If the perceived numerosity of pseudotransparent surfaces is conveyed by LIP, its activity should be modulated by the perceived depth order of the display and by figure-ground segmentation processes. It is currently debated whether the representation of numerosity in parietal cortex is abstract, i.e., independent of the form of presentation, or not (Cohen Kadosh & Walsh, 2009). Hence, it might be interesting to investigate whether the numerosity bias occurs only for the fields of dots we used in these experiments, or whether it would also affect other representations of numerosity.

The model by Tsirlin et al. (2012) assumes that a top-down signal increases activity in neurons representing the ground surface. The neural origin of this signal, representing the depth order in the display, is still unclear. The presented results indicate that it did not matter much, whether the depth order was defined physically by disparity or whether it was physically ambiguous and resolved by differences in motion direction. This means that the numerosity bias can be induced by a variety of depth order signals that could potentially originate in different brain areas (for a review see Parker, 2007). Neurons in the middle temporal (MT) area are sensitive to motion (Britten, Shadlen, Newsome, & Movshon, 1992; Newsome, Wurtz, Dursteler, & Mikami, 1985; Salzman, Murasugi, Britten, & Newsome, 1992) and disparity (Bradley, Qian, & Andersen, 1995; DeAngelis, Cumming, & Newsome, 1998) and are also sensitive to the ambiguous depth order in structure-from-motion displays (Bradley, Chang, & Andersen, 1998). Hence one possible source of the figure-ground segmentation in transparent motion might come from the MT area.

Conclusion

We provided evidence that the perceived numerosity of pseudotransparent surfaces is affected by the perceived depth order: numerosity is overestimated in the back and underestimated in the front. These findings have two physiological implications. First, the assignment of dots to the two surfaces is far from being perfect and numerosity might be computed on a global rather than local scale. Second, the numerosity of a surface is not computed independently of other surfaces in the scene but is highly dependent on figure-ground segmentation.

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